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THE RESISTANCE OF FISHES TO DIFFERENT CONCENTRATIONS AND COMBINATIONS OF OXYGEN AND CARBON DIOXIDE.

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I. INTRODUCTION.

In a recent article (Shelford and Allee, '13) entitled "The Reactions of Fishes to Gradients of Dissolved Atmospheric Gases" the authors discussed the physiological effects of gases in solution, on fishes, and presented a table showing the results of some preliminary experiments upon the resistance of fishes to low oxygen. They also report some experiments on the resistance to high concentrations of carbon dioxide.

It is the purpose of this paper to report some further experiments, which have been carried on in the same laboratory, with the purpose of determining what position, varying concentrations of oxygen and carbon dioxide, hold, in the physiology and thus the ecology and economy of fishes. The experiments herein reported were undertaken at the suggestion of Dr. V. E. Shelford, and have been carried on in his laboratory, with the use of part of the same apparatus (gas control) that was used in the experiments referred to above.

II. Plan of Experimentation.

The method followed throughout in these experiments has been, to introduce the fishes into water containing a constant and fatal concentration of oxygen, carbon dioxide, or combination of the two, and then to observe and record the reactions of the fishes, during the time which elapsed between introduction and death. This interval, between introduction and death, was found to be the only time that could be accurately determined for every species used. For this reason, it has been taken as the basis for the data upon which the conclusions of the paper are based. Shelford and Allee give, in their table of resistance to low oxygen, the time consumed between introduction and the turning of the fishes upon their backs. This method was tried in the experiments herein described, but it was found that with the species and conditions used, the "turning time" as they call it, did not, at least in so far as could at this time be determined, represent a definite and comparable time in the succumbing reaction. For example, it was found, that in many instances, the loss of equilibrium was a gradual and not a sudden process, an illustration being the case of the rock bass (*Ambloplites rupestris*). It was found that when two or more species were compared, first, with regard to turning time, and second, with regard to dying time, the comparisons did not show the same relations, in the majority of cases. Furthermore the catfishes and darters often died in a normal upright position, and displayed at no time a reaction that might be taken as the turning point.

It should be stated that Shelford and Allee observed their fishes under conditions which varied considerably from those of these experiments. They confined them in standing water, the temperature of which was not constant; the waste products were allowed to accumulate; and the gas concentrations varied as a result. In the following experiments, the fishes were observed in running water of constant temperature, and very slightly varying gas concentrations.

For the determination of the death point, the best criterion that presented itself was cessation of movement. To make certain that this point might safely be taken as the death point, individuals of different species were, from time to time, removed

and placed in fresh tap water, as soon as all movement had ceased. In none of these cases was there recovery or even further movement. However when a fish was removed while the movements were still faintly visible, it usually recovered and became normal once more. The nearness to the death point at which a fish might still be resuscitated varied with the species and with the individual. This variation was not fully determined. It is probable that if errors were made in determining the death point, they were upon the side of exceeding the actual time, for in nearly all cases, a fish was not regarded dead until no movement had been visible for from two to five minutes.

III. Apparatus.

The apparatus used in the experiments consisted of the gas control apparatus, already mentioned,[1] and of three large wide-mouthed bottles, with connections, etc. In brief the gas-control apparatus consists of a series of perforated pans, of boilers, and coolers. The water may be made to pass through the pans into the boilers and through the coolers, in the order named, or it may be turned directly into the boilers and on into the coolers. If gas is to be introduced, it is injected through a gas introducer, between the first and second coolers. In these experiments, the only gas introduced was carbon dioxide. This gas was introduced from the cylinders in which it is purchased. According to Shelford and Allee's analyses, the gas in these cylinders contains 99.4 per cent. carbon dioxide and .6 per cent. nitrogen (different cylinders may vary slightly). Variations in the oxygen concentration were obtained by treatment with the apparatus. The very low concentrations (.1 c.c. per liter) were obtained by boiling the water vigorously in the apparatus, and in order to do this it was necessary to start with the hot tap water of the laboratory. Because it was necessary to use the hot tap water in some experiments it was thought best to use it for all, and this plan was followed except in experiments with high oxygen (10 c.c. per liter). In these cases the cold tap water was used. In either case the temperature at which the water was used was the

[1] For full description of gas control apparatus, together with drawings, see Shelford and Allee ('13), p. 214.

same, for after the water had passed through the coolers in the apparatus, its temperature was the same as that of the cold water running through the coolers. In these experiments the temperature differed slightly on different days but was constant between 3 and 5 degrees centigrade.

By analyses, which are given in Shelford and Allee's paper, it has been shown that there is little chemical difference between the hot and cold tap water of the laboratory. At the time the analyses were made, however, it was found that the tap water after it had passed through the gas control apparatus, showed a slight increase in magnesium content. By later analyses, I have found that this increase was due to the accumulation of magnesium containing scale, in the boilers. To obviate this difference, I have kept the boilers free from any considerable accumulation of scale, and although no further analyses have been made since the beginning of the experiments, I do not think it likely that the effect of the apparatus upon the water has been any greater than the normal daily fluctuations of the water itself, excepting, of course, the differences that have been intentionally produced.

After passing through the gas-control apparatus, the water was led into a 2-liter wide-mouthed bottle (see Fig. 1). The introducing tube led the water to the bottom of this bottle, while the exit tube reached half way to the bottom. Thus all gas bubbles were retained in this first bottle and not allowed to pass into the experimental bottles. From bottle *A*, the water passed into a larger (8-liter) bottle, *B*. This was the first experimental bottle. From bottle *B*, the water was led into still another bottle, *C*, which was the second experimental bottle.

An experiment was conducted as follows. The gas-control apparatus was started and allowed to run from two to four hours, so that the gas concentrations might be regulated and made constant. The time required for this varied with what was to be done to the water. When consecutive tests, five to ten minutes apart, showed the concentrations to be those wanted, and constant, the hose connected with the outlet of the apparatus was slipped over the inlet tube of bottle *A*, the outlet tube of *A* connected with the inlet tube of *B*, etc. After the stream of

water had filled all the bottles and had been running through them for some time, during which time the corks of all the bottles had been sealed with modeling clay, it was again tested for concentration and constancy of dissolved gas. The samples were usually collected at the exit tube of bottle *C*. If the tests showed the desired concentration to be present and constant, fishes were quickly introduced, the corks rapidly replaced and resealed, and observations begun. Because of the fact that at

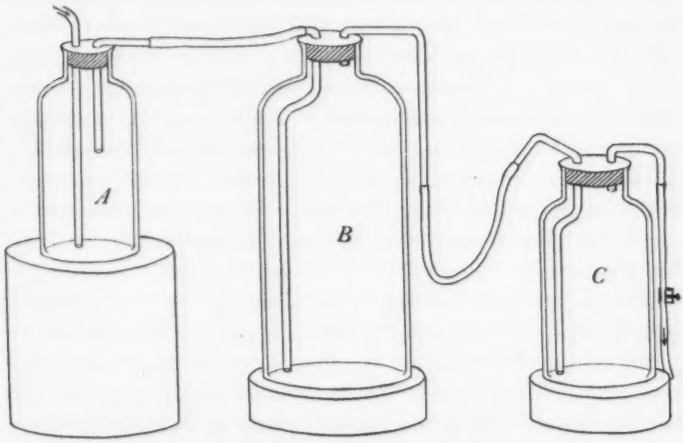

FIG. 1. Showing the arrangement of the catch bottle *A* and the experimental bottles *B* and *C*. In *A* the inlet and outlet tubes are so arranged that bubbles of undissolved gas are retained in the bottle. In *B* and *C* the inlet tubes lead the water to the bottoms of the bottles. The outlet tubes reach only to the bottoms of the corks. This insures thorough mixing of the water and thus conditions throughout the bottles are the same while the water is flowing through.

the beginning of an experiment one set of fishes usually demanded the entire time of the observer, but one set was introduced at a time. The second set was introduced and observed after the first set had passed through the first and more vigorous stages of the succumbing process.

In order to make certain that the water as it passed through bottle *B* was not affected to a measurable extent, by the presence of the fishes, a number of tests were made of samples collected at the exit tube of bottle *B*. None of these tests showed any

measurable difference in gas concentrations, as compared with samples taken at the exit tube of bottle *A*, and it is not probable that the salt content was appreciably affected by the fishes.

The method of analysis that has been used throughout is a slight modification of the standard methods of the Public Health Association.[1] In all cases, the collections of samples were made in narrow-necked bottles, through which the water was allowed to run for several minutes, with the delivery tube reaching to the bottom of the bottle. The bottles were kept corked as much as possible until after all the chemicals had been added. These precautions were essential, for in the case of low oxygen a sample may show 2–3 c.c. per liter, if collected and titrated in an open 250 c.c. graduated cylinder, while if tested as above, it may be found to contain but from .1–.15 c.c. per liter. For the carbon dioxide tests, a special bottle was devised. With this bottle, the cork was removed only to run in the sodium carbonate in titrating. This was always done immediately after the collection was made.

The water flowed through the bottles at the rate of from 500 to 600 c.c. per minute. This changed the water in the larger experimental bottle, once in about 15 min. and in the smaller once in 6 min. In both experimental bottles, the introducing tube led to the bottom, while the exit tube reached just to the under side of the cork. Finally, in order that the temperature of the water might not vary in the experimental bottles, a stream of cold tap water was kept running over each throughout the experiment. The number of fishes used in an experiment varied with their size. A smaller number was usually placed in the smaller bottle. The number in any single experiment varied from 2 to 10 and about 160 were killed, in all. About 25 experiments were performed; the shortest occupied from two to three hours and the longest five to seven days.

The fishes used in the experiments were taken in one of the small creeks near Chicago and were for the most part experimented upon before they had been in the laboratory aquaria for more than two or three days. In no case had they been in captivity for longer than three weeks. In the laboratory they

[1] See *Jour. Infectious Diseases*, '05, supplement No. 1.

were kept in running tap water and there was practically no mortality. In all some fifteen species were used. In a few instances, few individuals were available and in these cases the data will not be presented unless particularly suggestive.

IV. Reactions of the Fishes.

The experiments were of six kinds, this number resulting from the different combinations of gases, those being selected which it seemed would be most likely to give significant results. They were (1) low oxygen (0.1–0.15 c.c. per liter) and high CO_2 (35–50 c.c. per liter); (2) low oxygen and alkaline water (0.5 c.c. N/20 HCl made neutral); (3) low oxygen and medium CO_2 (15–17 c.c. per liter); (4) low oxygen and low CO_2 (about 1 c.c. per liter); (5) medium oxygen (3–4 c.c. per liter) and high CO_2; and (6) high oxygen (8–10 c.c. per liter) and high CO_2.

All the concentrations used are found at times in natural waters. Birge and Juday ('11, pp. 144–169) report concentrations of carbon dioxide for Wisconsin lakes, which vary from about −7 c.c. to nearly +35 c.c. per liter. They also report concentrations of oxygen varying from 0 to 15 c.c. per liter. On page 89 (*l. c.*) they report concentrations of carbon dioxide as high as 47.8 c.c. per liter, in the ground waters of the state. Allee (unpublished) in tests of the water in the series of ponds along the south shore of Lake Michigan has found 40 c.c. per liter of carbon dioxide. In analyses of the water of these same ponds, I have found concentrations of oxygen varying from 1 c.c. to 12 c.c. per liter.

It is probable that the extreme concentrations, as low oxygen (0.1 c.c. per l.) and high carbon dioxide (35–50 c.c. per l.) are not in any sense general conditions, but concentrations not so extreme are of frequent occurrence. Birge and Juday state that conditions of low oxygen and high carbon dioxide may exist for long periods in the deeper waters of the Wisconsin lakes, but the influence of such concentrations upon general fish distribution is probably not so great as that of smaller but more widely distributed concentrations.

The presence of high and low concentrations of carbon dioxide is affected by many factors such as vegetation in the water,

character of surrounding soil and incoming water, depth of the water, season of year, daily temperature, animals present, decaying organic matter, rainfall, exposure of the surface of the water to winds. With so many factors affecting the gas concentrations, they will vary greatly even within the same body of water, at any given time. Birge and Juday (*l. c.*) have found this to be especially true in small deep lakes, for different depths. In my own analyses of the waters of the Chicago region, I have found horizontal differences that are also somewhat striking. For instance the lower end of a fifty-foot pool in a small creek may contain 5 c.c. per liter of oxygen less than the water of the upper end. Such variations are common and their influence upon fish distribution must be marked.

In describing the reactions of the different fish species, it will be possible to give a general account which will stand in the main for all the types of experiments. Given in chronological order, the reactions were as follows: Upon introduction into the treated water, the activity of the fishes was usually increased for a short time. This increase was due in part to the handling, but also in part to the stimulation of the water, since fishes introduced in the same manner into normal water were not so active. The greatest increase in activity came with introduction into the low oxygen (0.1–0.15 c.c. per l.) water. The period of activity usually lasted for only 5 to 10 seconds at which time some of the fish occasionally lost their equilibrium (*e. g.*, smallmouth bass), or they sank to the bottom or floated in the water in an upright position. In all of the experiments, and especially in the low oxygen, the opercular movements at once became much more vigorous and continued so up till near the death point. The time period between introduction and the appearance of signs of loss of equilibrium varied with the combination and concentration of the gases present. In general this period varied directly as the lowness of the oxygen concentration or the highness of the carbon dioxide.

The fishes, upon sinking to the bottom, or upon becoming quieter in the water above, rested for a longer or shorter period and then began to "nose" more or less actively about the bottle. Gulping occurred almost from the beginning. This is a normal

reaction to some extent but in the experiments the vigor and frequency of the gulping was very noticeable, and gas bubbles were often ejected at the gulps. The fishes now passed through a period of alternating rest and activity. During the early phases of this period, activity was in the ascendency; later rests occupied most of the time. The resting periods lengthened with the gradual loss of equilibrium. The first sign of "staggering" was a falling to a vertical position with the head up. The fish gradually sank to this position and at first made swimming movements which caused it to resume a horizontal position. Later the restoratory movements were not made until the fish came in contact with the bottom. Still later the contact stimulus failed to cause a response and the fish came to rest on the bottom, lying either on its side or on its back. The gill movements were usually still strong and regular. The fish now lay on the bottom, making only occasional swimming movements.

In the low oxygen experiments, the movements of the fishes often became convulsive and uncoördinated before equilibrium was lost, and as time passed, this phenomenon became more and more noticeable. Carbon dioxide, in the concentrations used, did not cause much lack of coördination, but it has been demonstrated that very high CO_2 (100 c.c. or more per l.) will quickly produce this effect. The effect of the carbon dioxide in the concentrations used was that of an anæsthetic which stimulates in small amounts, or at first, but later anæsthetizes. In this connection it was noted that the fishes that were the first to succumb to the carbon dioxide were usually those that displayed the greatest activity.

As the fishes became more and more overcome, the gills developed irregularity in movement; gulps and extra large opercular movements became frequent; later the gills became more or less distended and stiffened, and the movements infrequent. Thus in cases where the gill movements averaged 9–10 in 10 seconds at first, there might now be an average of one or less in the same period. At about this time the gill movements took on a jerky mechanical appearance which continued until they stopped altogether. In nearly all cases, after the gill movements had stopped, life was still indicated by movements of the fins and

especially the pectorals, which twitched or waved somewhat regularly for several minutes after the opercular movements had ceased. With the final cessation of movement upon the part of the fins, the fish was considered dead. This final cessation of all movement was often preceded in the low oxygen experiments, by a sudden violent paroxysm, during which, the fish "scooted" about the bottle in a blindly convulsive manner.

V. Resistance of the Fishes.

The resistance of the fishes varied with the individual, with the species, and with the size. No reliable data were obtained with regard to individual variation, because of lack of knowledge of the previous history of the animals. Specific and size differences in resistance were however great enough to cover up, to a considerable extent, the unknown individual factor and are to this extent indicatory. With regard to the size (*i. e.*, weight) in the same and different species, it was found that small fishes showed a greater resistance per unit of weight than did the larger ones. At the same time, the larger fishes, because of their excess weight, usually lived longer per individual. These two sets of reactions are clearly shown in the tables which follow.

Table I.

Showing the Comparative Resistance of Large and Small Fishes of the Same Species to Low Oxygen (.1–.15 c.c. per Liter) and Medium Carbon Dioxide (15–17 c.c. per Liter).

Species.	No. Fish.		Av. Length in Cm.		Av. Weight in Grams.		Av. Dying Time per Fish in Min.		Av. Dying Time per Gram in Min.	
	Large.	Small.	Large.	Small.	Large.	Small.	Large.	Small.	Large.	Small.
Rock bass (*Ambloplites rupestris*)	2	2	12.5	5.0	40.7	2.3	371.0	46.5	9.1	20.2
River chub (*Hybopsis kentuckiensis*)	4	2	10.3	6.5	15.6	3.0	113.5	103.0	7.2	34.3
Blunt-nosed minnow (*Pimephales notatus*)	2	1	8.5	7.5	6.8	4.3	74.5	67.0	10.9	14.9
Red horse (*Moxostoma aureolum*)	2	2	9.2	7.2	11.0	3.7	45.0	88.0	4.0	23.8

Table I. gives the results of a few typical experiments in which low oxygen (0.1–0.15 c.c. per l.) and medium carbon dioxide

(15–17 c.c. per l.) were the fatal factors, and illustrates the relative dying order of the large and small individuals of the species used. It will be seen that the larger fishes lived longer per individual, but a shorter time per gram, than the smaller ones. This is shown clearly in the last four columns. That the dying time per individual varies directly, while the dying time per gram varies inversely as the weight of the individual, is still more clearly shown in Table II., which gives this relation for two of the species, namely the rock bass (*Ambloplites rupestris*) and the common shiner (*Notropis cornutus*).

In Table II. the relation holds very closely in the case of the shiner, but seems to break down in the case of the larger individuals of the bass. This apparent variation is to be ex-

TABLE II.

SHOWING THE RESISTANCE OF DIFFERENT-SIZED FISHES OF THE SAME SPECIES TO LOW OXYGEN (.1–.15 C.C. PER LITER) AND HIGH CARBON DIOXIDE (35–50 C.C. PER LITER).

Species.	No. Fish.	Av. Length in Cm.	Av. Wt. in Grams.	Av. Dying Time per Fish in Min.	Av. Dying Time per Gram in Min.
Rock bass (*Ambloplites rupestris*)	1	4.4	1.9	20.0	10.5
	1	4.5	2.0	22.0	11.0
	1	5.0	2.1	23.0	10.9
	1	10.5	20.0	103.0	5.1
	1	12.0	31.0	45.0	1.4
	1	14.0	45.0	93	2.1
Common shiner (*Notropis cornutus*)...	1	4.5	.6	15	25.0
	1	8.0	4.5	23	5.1
	1	8.5	5.5	37	6.7
	2	9.5	7.0	39	5.5
	1	12.3	17.8	40	2.2
	1	12.5	21.0	45	2.1

pected in very large fishes of any species, however, for if the unit weight of the fishes loses power of resistance with increase in age, sooner or later there will come a stage in the life cycle, where the increase in weight, which for a time offsets the decrease in resistance, will diminish and perhaps stop altogether, while the ageing process will go on. Thus the individual resistance curve, which at first rises more or less rapidly, will, at some point, reach its maximum and begin to decline. The fishes will then

be less resistant per individual than smaller fishes of the same species. That such is the case with the rock bass is indicated in the table.

Now if this relation holds in general, the expectation would be, that young fishes of a large species will possess greater powers of resistance than adult fishes of another but smaller species, when the young of the larger and the adults of the smaller species are of the same weight. That such an assumption is tenable is illustrated by nearly all the experiments in which such young and adults occurred. For purpose of illustration, a table showing the results of a series of such experiments is inserted.

Of the species occurring in Table III. the darters and the shiner are small, seldom weighing more than 2 or 3 grams. The red horse is a large species but is easily killed by slight changes in the content of the water (Forbes and Richardson '08, p. 91). Adults of the remaining three species are rather large and resistant.

TABLE III.

SHOWING THE RESISTANCE OF SMALL FISHES TO LOW OXYGEN (.1–.15 C.C. PER LITER) AND LOW CARBON DIOXIDE (1 C.C. PER LITER).

Species.	No. Fish.	Av. Length in Cm	Av. Wt. in Grams.	Approx. Adult Wt. in Grams.	Av. Dying Time per Fish in Min.	Av. Dying Time per Gram in Min.
Darter (*Etheostoma cæruleum*)	3	5.4	2.3	2–3	40	17.3
Red horse (*Moxostoma aureolum*) ...	2	7.0	3.3	2500.0	52.5	15.9
Shiner (*Notropis atherinoides*)	8	5.0	1.58	1–2	104.0	65.7
Rock bass (*Ambloplites rupestris*) ...	2	6.0	2.0	300.0	125.5	62.7
Common shiner (*Notropis cornutus*)..	7	4.8	.79	20.0	195.0	246.7
River chub (*Hybopsis kentuckiensis*).	2	4.5	.95	30.0	250.0	263.1

A glance at the table will show that although the young of the rock bass, the river chub, and the common shiner, weighed less than the darters, and only in the case of the rock bass more than the shiner (*Notropis atherinoides*), still they proved to be more resistant than the adult darters and shiners, by a considerable margin.

Because of the fact that there was often a break in the increasing weights of the fishes used, and because it was found to be hardly possible to compare species one with another, if the

TABLE IV.

SHOWING THE RESISTANCE OF DIFFERENT SPECIES OF FISHES TO FATAL CONCENTRATIONS AND COMBINATIONS OF OXYGEN AND CARBON DIOXIDE. (FISHES WEIGHING OVER 5 GRAMS AND BEING FROM 8 TO 26 CM. LONG.) LOW O_2 = .1–.15 C.C. PER LITER, MED. O_2 = 2–3 C.C. AND HIGH O_2 = 8–10 C.C. PER LITER. FOR CO_2, LOW = 1 C.C., MED. 15–17 C.C. AND HIGH 35–50 C.C. PER LITER.

Species.	Resistance to												General Average of the Resistances to the Different Factors. The General Average Indicates the Comparative Resistance of the Different Species.	
	1. Low Oxygen and High CO_2.		2. Low O_2 and Alkaline Water.		3. Low Oxygen and Medium CO_2.		4. Low Oxygen and Low CO_2.		5. Medium O_2 and High CO_2.		6 High O_2 and High CO_2.			
	Dying Time per Fish in Minutes.	Dying Time per Gram of Fish in Minutes.	Dying Time per Fish in Minutes.	Dying Time per Gram of Fish in Minutes.	Dying Time per Fish in Minutes.	Dying Time per Gram of Fish in Minutes.	Dying Time per Fish in Minutes.	Dying Time per Gram of Fish in Minutes.	Dying Time per Fish in Minutes.	Dying Time per Gram of Fish in Minutes.	Dying Time per Fish in Minutes.	Dying Time per Gram of Fish in Minutes.	Dying Time per Fish.	Dying Time per Gram of Fish.
Common sucker (*Catostomus commersonii*)	.....	.....	.....	.....	49.3	8.2	350.0	1.8	.....	.....	.....	.....	.....	.....
Red horse (*Moxostoma aureolum*)	15.0	1.5	20	2.0	45.0	4.0	100.0	14.3	1,865	124	2,072	210	686.1	59.3
Small-mouth bass (*Micropterus dolomieu*)	40.0	3.9	68	8.0	87.0	10.9	70.0	7.2	1,085	54	3,995	790	898.3	147.1
Green sunfish (*Lepomis cyanellus*)	182.0	6.4	210	9.5	215.0	14.3	225.0	11.5	995	90	4,110	326	989.5	76.3
Blunt-nosed minnow (*Pimephales notatus*)	32.0	5.8	50	8.5	74.5	10.8	89.0	16.7	2,902	560	3,995	799	1,190.4	233.4
River chub (*Hybopsis kentuckiensis*)	50.0	4.0	70	5.3	113.5	7.2	68.7	3.1	3,741	366	4,092	511	1,322.5	149.4
Common shiner (*Notropis cornutus*)	40.0	3.4	65	6.3	96.0	10.4	107.0	12.4	4,997	557	5,666	679	1,828.5	228.1
Rock bass (*Ambloplites rupestris*)	88.6	2.8	145	6.3	371.0	9.1	404.2	9.5	8,285	368	8,992	391	3,047.6	115.4
Black bullhead (*Ameiurus melas*)	1,318.0	18.0	.....	.....	.....	.....	1,365.0	18.3	.....	.....	.....	.....	.....	.....

young were averaged with the adults, the fishes were divided into two groups upon the basis of weight. The dividing line between the groups fell more or less naturally at about 5 grams. Upon calculating the data for the two groups thus formed, it was further found that each group illustrated much the same specific relations, and for this reason but one group, that of the larger or adult fishes, will be discussed. In Table IV. is indicated the resistance of a number of species to different experimental conditions.

Table IV. illustrates the following points: (1) the relative specific resistance of the fishes to the six artificial environments taken singly (vertical columns, except last two); (2) the relative specific resistance of the fishes to the environments taken together (last two vertical columns); (3) the efficiency of each environment as a death-producer for the species used; (4) the antagonistic action of oxygen and carbon dioxide when in the same solution (vertical columns 5 and 6); (5) that an optimum carbon dioxide concentration probably exists for the fishes in question (columns 2 and 4); and (6) that of the concentrations used, the low oxygen was more detrimental to the fishes than the high carbon dioxide (columns 1 and 3).

With regard to the relative resistance of the different species to the environments taken singly, attention is called to the fact that the order varied with the different combinations. This indicates that fish species vary in their resistance to any one factor, the species that is more resistant in one environment being less so in another. The relative resistance of the species to the environments taken as a whole is shown in the last two columns. The order was obtained by averaging the resistances to the single environments. Reading from right to left along nearly any horizontal row of figures will show an increasing resistance of the species to the different environments as arranged in the table. The most fatal combination used was low oxygen (0.1–0.15 c.c. per l.) and high carbon dioxide (35–50 c.c. per l.), and the least fatal, high oxygen (8–10 c.c. per l.) and high carbon dioxide. That this would be the result has already been intimated by Shelford and Allee ('13).

If in the table, column 5 be compared with column 6, it will be

seen that the presence of the larger amount of oxygen increased the resistance of the fishes to the high carbon dioxide. Hill and Flack ('10) report this same antagonistic reaction between the two gases and decide from some rather conclusive experiments that the partial pressure of oxygen influences both the higher and the lower limit of carbon dioxide which can be endured by the organism.

A comparison of the second and fourth columns of the table will show that the fishes died more quickly in water that was slightly alkaline than they did in water that was slightly acid. The exact meaning of this difference is not clear. It may be that the alkaline water has some detrimental local effect upon the gills, or it may be that the neutrality mechanism (Henderson, '13) of the fishes is more quickly affected for the worse in the presence of low oxygen, when the water is slightly alkaline than when it is acid. At any rate the results indicate that the fishes have a carbon dioxide optimum. This agrees with Bottazzi's investigations for tissues, as quoted by Jerusalem and Starling ('10). They quote him as saying that "possibly a certain partial pressure of carbon dioxide in the liquid or blood, bathing the tissues, may represent the most favorable condition for the exhibition of the tissues' activity, and that in every tissue it ought to be possible to find an optimum tension of carbon dioxide at which the tissue would do its best work."

A comparison of the different columns in Table IV. will show that the more effective factor in producing death was the low oxygen. One good illustration of this will be noticed in the case of the black bullhead (*Ameiurus melas*) which occurs in columns one and four. In these columns are presented results for two sets of conditions, which differed only in the concentration of the carbon dioxide, the other factor being low oxygen in both cases. It will be seen that the bullhead lived nearly as long in the high carbon dioxide experiment as it did in the low. This indifference of the fishes to variations in carbon dioxide under these conditions is not so clear with the other fishes, but it seems to be generally true that 0.1 c.c. per liter of oxygen will produce death sooner than 50 c.c. per liter of carbon dioxide. It should be noted however (Shelford and Allee, '13) that most fishes

detect and react to carbon dioxide even in quite low concentrations quicker than they do to low oxygen. It has already been stated that higher concentrations of carbon dioxide (*e. g.*, 100 c.c. per l.) are more fatal than 0.1 c.c. per liter of oxygen.

VI. General Discussion.

There are a number of questions relating to the physiology of fishes that are touched upon by the results of the foregoing experiments, but no attempt will be made to discuss them at this time, for the data are far too incomplete. There are, however, certain ecological and economic bearings, which may be taken up briefly, with some profitable results.

From the experiments described in this paper, and from those of other workers (Shelford and Allee, '13; Ransom, '66) we may conclude that, in general, the distribution and at times the existence of fishes depend upon two things, namely, (1) the resistance of the fishes to any condition or set of conditions in the environment, that may vary so as to become harmful; and (2) the reaction of the fishes to any such varying condition or set of conditions.

Of these two factors, namely, resistance and reaction, neither can be said to be all-important in any environment, and in most environments the two are inextricably woven together. In the following discussion no attempt will be made to separate the two, but the factor of reaction and behavior will be emphasized over that of resistance, for it seems to me that future investigation must show fully, what previous investigation has already indicated (Shelford, '11; Shelford and Allee, '13*a*), that the reactions of fishes to the conditions of the environment are more vital in determining their distribution and persistence than is their power of resisting adverse conditions.

With regard to behavior and resistance, the fish life cycle can be broken up into four rather distinct periods: (1) the breeding behavior of the adults; (2) the resistance of the eggs and fry; (3) the behavior and resistance of the young fishes; and (4) the resistance and general behavior of the adults.

1. *The Breeding Behavior of the Adults.*—It is generally known that the eggs and fry are stages of relatively low resistance. It

is therefore a matter of much importance that the adults choose a location for depositing the eggs that will enable them to develop normally, and which will prove efficacious for the first stages of growth of the fry.

That the adults make the selection successfully in a majority of cases is undoubtedly true and the fact that the conditions at the breeding grounds may be very different from those of the normal habitat does not seem to interfere with the choice. The conditions necessary for early stages of different species vary widely. Thus the adults of two or more species may live in the same general habitat up to the breeding season when the process of selection of suitable breeding grounds often results in their becoming widely separated. This results in the eggs of the different species being deposited, and the young hatched, under conditions which may differ greatly, but which in most instances prove to be the best for the development of the first stages of each species.

By what process the adults of each species are enabled to select from the great variety of combinations of conditions that combination that is best suited to the development of their own eggs and fry is a matter for investigation. It is probably true that, to a large degree, the choice is a result of reactions, chemical and otherwise, to the factors of the environment. Everman ('98) states that in Louisiana the blue catfish (*Ictalurus furcatus*) and goujon (*Leptos olivaris*) are influenced in their movements by the temperature of the water. During the winter they come farther down the river, where the water is warmest, and in the summer run further up stream or retire to the deeper waters. In some recent experiments with fishes in temperature gradients I have found that many species are very sensitive to slight differences in the temperature of the water, detecting and reacting to differences as small as 1 to 2 degrees C. Gurley ('02) thinks that temperature together with salinity are the factors by which the salmon and other fishes which come from salt into fresh water to breed are enabled to find the freshwater streams.

Green ('09) states that salmon, when coming into fresh water during the breeding season, often spend from 2 to 4 days swimming back and forth in the brackish water before passing on into

the streams. Some fishes select certain kinds of bottom for nesting sites, and in doing so probably react to light, temperature and dissolved gases.

What particular factors are most important in the selection of breeding sites is not at present clear; it will probably be found that many factors are acting in most cases, but that some few factors are of such common importance in the breeding reactions of large groups of fishes that they may be used as an index to the breeding behavior of such groups.

In connection with the breeding behavior of fishes there are, besides the general reactions involved in the selection of suitable situations for depositing the eggs, a great number of more specific reactions which are often of the utmost importance in the successful rearing of the new generation. Such reactions are familiar and are illustrated by those of nest-building, aerating the eggs by different devices, guarding the eggs, etc.[1]

2. *Resistance of the Eggs and Fry.*—In spite of the reactions of the adult fishes, which tend to protect the eggs, it is true that of the many thousands that one female may deposit, but very few ever reach the adult stage (Paige, '08) and in most cases the greatest mortality comes at the period when the eggs and fry are developing, (Anthony, R., '08). At this time the relative resistance of the fishes is very low, and many of the eggs probably do not develop because of too great variation in the surrounding conditions; others may develop into abnormal forms which are unable to survive the juvenile period.

Ransom ('66) has shown that a certain concentration of oxygen is necessary in the development of fish eggs; he has also shown that carbonic acid arrests development and may result in the production of abnormal forms which never reach the free swimming stage. Milner ('72) observed that a supply of oxygen was necessary in the successful shipping of eggs, and Loeb ('12) states again the results of some experiments performed upon the eggs of the sea-urchin, in which he found that these eggs can develop only in the presence of free oxygen, that if the oxygen is withdrawn development stops, but begins again if the oxygen is readmitted. He also states that the process of fertilization

[1] See citations in Shelford, "Ecological Succession," III., '11.

probably results in a decided increase in the oxidations of the egg. This increase in the oxidations would tend to make the eggs more sensitive to adverse conditions, especially in low oxygen water, and it is very probable that eggs must at times be subjected to severe conditions because of this.

3 and 4. *Resistance and Reactions of Young and Adult Fishes.*—Of the importance of the resistance powers of fishes in general, in waters where there is no escape from the harmful conditions, there can be no doubt. Also the relative resistance of young and adult fishes is a matter of consequence. In the experiments, described in this paper, it was shown that concentrations of detrimental factors, which are long in affecting adult fishes, may prove fatal to small fishes of the same species, in a comparatively short time. From this it will be seen that, ecologically and economically, the fact that young fishes are more resistant per unit of weight cannot be considered of great importance.

With regard to the resistance of fishes to environmental complexes it is possible to separate environments into two general classes, namely, (1) environments whose conditions are constant or nearly so from season to season and year to year (large bodies of water); and (2) environments where the conditions fluctuate considerably from season to season or from year to year (smaller lakes and streams).

If we consider fishes in their relation to these two types of environments, with resistance as the factor in the foreground, we must look upon the matter of fish existence and distribution as determined by the ability of fishes to withstand the constant conditions in class 1, or the varying conditions in class 2. This then forces us to the conclusion that the matter of fish existence in a given area is one of little flexibility. If, however, we consider the behavior factor as important, it will be seen at once that the matter of fish persistence is now determined by the reactions of the fishes to the two sets of conditions, and becomes at once flexible, because of the fact that the fishes may avoid adverse conditions by moving out of them.

That fishes will react in this way in natural waters is no longer a question of doubt. Both adult and young fishes are sensitive to detrimental concentrations of oxygen and carbon

dioxide, as was clearly shown in the experiments described in this paper, and that they will turn back from such concentrations has been shown by Shelford and Allee ('13) and in some later experiments by myself. With regard to the comparative sensitiveness of young and old fishes, Wiegelt ('85) found that young fishes were more sensitive to ammonia than adults, and Shelford and Allee found the same relation to be generally true for their fishes, in the cases of oxygen and carbon dioxide. Such being the case, in natural lakes and streams fishes would generally find a way out of areas of adverse conditions (Green, '09) if the conditions did not appear too rapidly, and the first to become active in seeking escape would be the young fishes.

Many complications suggest themselves in a consideration of the ability of fishes to persist in a given environment. One will be considered as suggestive. What will be the result of planting a species of fishes in an environment, in which by its combined resistance and behavior reactions, the species is able to reproduce, but at a great disadvantage, as for instance high egg and fry mortality?

This question is tied up with the matters of acclimatization, adaptation, etc. There are two main possibilities. First, the adverse conditions may result in the resistance of each succeeding generation being raised; or second, the result may be a lowering of the specific resistance, with each succeeding generation. Lowering the resistance of the species will soon lead to extermination; raising it may result in the species' becoming prolific in waters that at first threatened extermination.

Whether fishes adjust themselves to conditions is not yet clear. There is evidence that they may adjust, in the fact that many lower forms are able to do so. Wood Jones ('12) states that corals of the same species show great variation in structure in different environments; Moore ('97) states that very young oysters will become acclimated to new conditions when older ones will not, and ('08) he further states that "commercial sponges are very susceptible to the influences of the environment and when transplanted from one place to another speedily change in character." Whether fishes will so adjust is a matter for investigation and especially since, so far as is known, fishes are not particularly plastic at any stage.

To determine the efficiency of a given body of water as a fish-producer requires the solution of a large number of problems such as the above, and many of these problems demand that the relative importance of resistance and reaction, in fish distribution and existence, be known. In the discussion thus far, resistance of fishes has been shown to be of considerable importance in fish survival, under certain conditions and at certain stages of development. That fish reaction is the more important factor, however, is indicated largely by one fact, namely, *adverse conditions in natural or artificial fish environments are seldom so general or so sudden in appearance that the fishes cannot escape them, at least to an extent sufficient for survival, by making the proper reactions, and observation and experimentation indicate that fishes, in the majority of cases, make such reactions.* It seems pretty well established that fishes regulate their own distribution, and thus indirectly their existence, largely through their reactions to the environmental factors which they encounter. In other words, fishes seldom put their resistance powers to the test, so long as there is a way out of the disturbing conditions. It follows that resistance of fishes becomes a life and death matter, only when adjustment cannot be made by a behavior reaction, and such situations are rare in the life cycles of most fishes.

On the other hand, fish reactions are an important factor even in the smallest and most enclosed bodies of water, provided the waters are able to support fishes at all. In ponds, for instance, the fishes may be able to withstand the stagnancy of the dry season, by coming to the surface, gulping the surface film, burrowing into the bottom, etc. (Kendall, '10). In some fish environments, vertical differences in conditions are most important in their effect upon fish reactions. In small lakes and streams horizontal conditions are important. In such waters there are areas of vegetation, muddy bottom, sandy or gravelly bottom, ripples, pools, etc. Where such conditions are present there is considerable opportunity for the selection of habitat, upon the part of the fishes, and that they exercise such choice has been demonstrated by Shelford ('11*a*). As a result of the choosing, we find the darters, for example, in the swift-flowing rock-bottomed ripples, while the suckers in general

are to be found only in the muddy-bottomed pools. Moreover the two groups of fishes seldom encroach upon one another's environments, even though they be directly adjoining as in streams where ripples and pools alternate.

If fishes are kept to their own environments by rather definite reactions to conditions, then should the conditions begin to change, as for instance, the pool begin to fill with resulting changes in dissolved gases, temperature, light, current, etc., the fishes will move away and will not settle down until they reach, more or less accidentally perhaps, but also by definite reactions at times, another set of conditions, that is similar to that which they formerly inhabited. Furthermore, the conditions might change slowly, or but a little, so that the young fishes and the adults of the more sensitive species would be the first and perhaps the only ones to leave. In this case the result would be the slow, partial and perhaps complete depopulation of the area, provided the adverse conditions prevented the entrance of other fishes from the outside.

Shelford and Allee ('13*a*) found that certain species of fishes will turn back quite definitely from concentrations of carbon dioxide as low as 5–7 c.c. per liter, and from oxygen as high as .7–1 c.c. per liter. This being the case, the above illustration need not be considered as at all hypothetical, for concentrations such as those indicated may be found in certain parts of nearly any system of rivers and lakes. Often the adverse conditions are seasonal in occurrence, or they may appear only when certain factory and sewage wastes are introduced into the waters (Marsh, '07), but whatever the time or cause, the result must be the partial or complete depopulation of the area so long as the adverse conditions continue.

It should be noted in this connection, that small variations (*e. g.*, 5–10 c.c. CO_2 per liter) from the normal, probably in many instances, produce in the long run effects similar to those produced by greater variations (*e. g.*, 25 c.c. CO_2 per liter) in relatively short periods. From the standpoint of ultimate persistence of the fishes, it makes little difference whether they die within an hour, a week, a month, or do not die at all, but merely stop reproducing successfully, the final result must be the same,

i. e., the disappearance of the fishes from the area so long as other fishes do not come in from the outside. Furthermore the fishes might continue to reproduce more or less normally, without preventing depopulation, if the adverse conditions caused the young fishes to leave the area.

We can say then that in the long run the fish population of an area will vary directly as the concentration of adverse conditions, or that (1) the moving out of the fishes from the area, and (2) the turning back of outside fishes which tend to enter, will at some concentration of adverse conditions inevitably result in complete depopulation. Furthermore, so long as such reactions are possible, the only part played by resistance will be that the least resistant fishes, since they are usually also more sensitive, will move out or turn back first. In neither case need the matter of dying time be taken into consideration.

Summary.

1. Fishes die from lack of dissolved oxygen or excess of dissolved carbon dioxide.

2. Oxygen in large amounts (10 c.c. per l.) antagonizes the detrimental effect of high carbon dioxide (50 c.c. per l.).

3. The action of detrimental concentrations of carbon dioxide and of oxygen is first to stimulate, and if detrimental enough, to later cause coma.

4. Low oxygen (0.1 c.c. per l.) in alkaline water causes death sooner than low oxygen in slightly acid water. This suggests that the fishes have a CO_2 optimum.

5. The resistance of the fishes to fatal concentrations and combinations of oxygen and carbon dioxide varies with the individual, with the species, and with the size (*i. e.*, weight).

6. Small fishes are more resistant per unit weight than are large ones. This fact is not particularly important ecologically or economically.

7. Ecologically and economically, it does not matter whether the fishes in a given body of water die within a minute, an hour, a week, or do not die at all but merely fail to reproduce successfully; the final result must in any case be the same, *i. e.*, the disappearance of the fishes from the area, unless new stock be constantly added.

8. Fish resistance is important in certain enclosed bodies of water, and at certain periods of the life cycle (egg and fry stages), but the more important factor in fish distribution and survival is the reaction of the fishes to the environment.

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BEHAVIOR OF THE COMMON ROACH (PERIPLANETA ORIENTALIS L.) ON AN OPEN MAZE.

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TECHNIQUE.

The maze (Fig. 1) used in these experiments was constructed out of a sheet of copper 13.5 inches long and twelve inches wide. Each runway is one inch wide and has neither sides nor top; and between each adjacent runway there is a space one and a half inches wide. This maze contains four blind alleys; two which are straight (Fig. 1, *A*, *B*), one which is L-shaped (Fig. 1, 8 *DE*), and one which bears three culdesacs (Fig. 1, 9 10 11

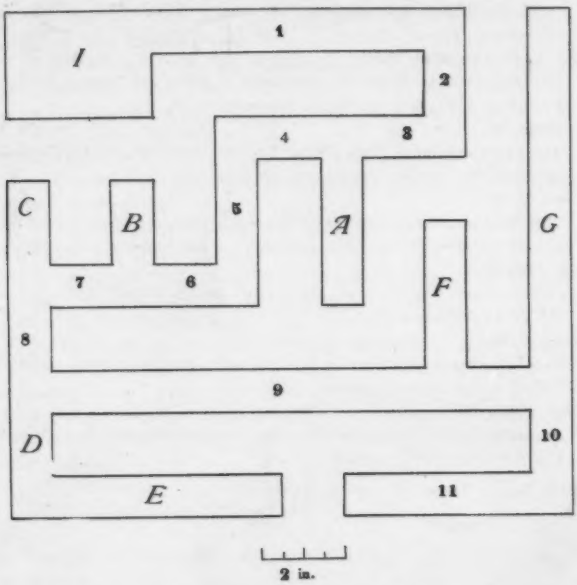

FIG. 1. A diagram of the maze used. *I* is the platform on which the roach is placed. *C* is the point from which the incline departs. The numerals 1–7 indicate the direct passageway to *C*. *A* is blind alley I., *B* is blind alley II., 8 *DE* is blind alley III. and 9 *FG* 10 11 is blind alley IV. of the tables.

FG). When in use the maze is supported, in a horizontal position, by glass pillars which rest in wide pans of water (Fig. 2). These pillars were made by inserting glass stirring rods in the corks of wide-mouth bottles. When thus supported, the maze was about eight inches above the surface of the water which extended beyond it, in all directions, to a distance of eight to twenty inches. To facilitate the taking of accurate notes the parts of the stage were labeled as indicated in Fig. 1.

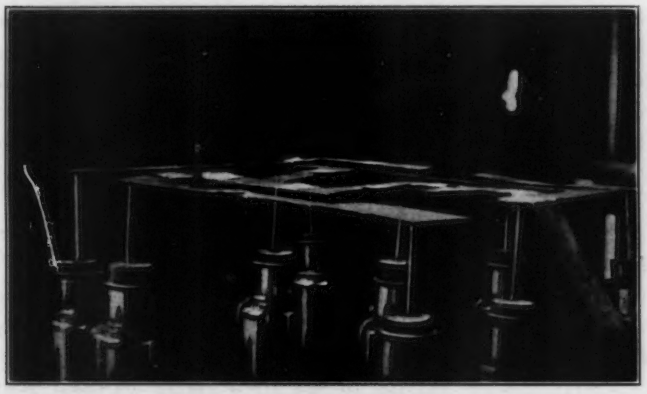

FIG. 2. Photo showing the maze and the upper portions of its support as arranged for use.

These experiments were conducted, in the summer time, in an out-of-doors insectary, the whole north wall of which, except a narrow strip for a door, was constructed of wire netting. The three other walls were without either windows or doors, hence this north opening was the only source of light. Except in the few special cases mentioned in the body of this article, the maze was always arranged with the side *I*1 on the north and parallel to that side of the house.

As originally planned the experiments were to test the ability of the roach to learn to go by the shortest route from the portion of the maze marked "*I*" to a dark box placed at some definite place on the maze. A few preliminary experiments demonstrated that the box did not make a satisfactory goal. Some insects on reaching the box would enter it and remain therein; others would

climb up to the top of it, meander around and then descend and go to some other part of the maze. Hence a cardboard incline, extending from some definite part of the maze to the jelly glass that had served as a cage for the roach, was substituted for the dark box.

This same series of experiments taught me that the best place for the incline to leave the maze was the point labeled "*C*." To be of value the incline should be located where the roach, in roaming about the maze, is sure to accidentally discover it. It was found that, in almost all cases, a roach, on reaching the junction of 7, *C* and 8, turned into 8 and, after passing into *D* and often into *E*, retraced its steps and entered *C*; hence an incline placed at *E* would have been too easy a problem. It was noticed that roaches seldom entered 9; hence to place the incline at the extremity of either 11 or *G* would be making the task too difficult. *C* seemed the golden mean.

The roaches used as the subjects of these experiments were isolated in jelly glasses and given an abundance of food. No roach was used in an experiment until it had been in its jelly-glass cage for several days. This was done to get the roach accustomed to confinement and to my presence. The roaches used were females varying in size from young ones ten millimeters in length to full-grown individuals.

The roach to be tested was always placed on *I*. This was done in two different ways. Sometimes the hind leg of a roach was grasped in a pair of forceps and the roach placed on *I*; at others, by means of forceps, the roach was transferred from its glass cage to a narrow cylindrical beaker. This glass was then covered with a small piece of paper and the whole inverted on the maze at *I*. The paper was then removed, and, as soon as the roach quieted down, the cylindrical glass was removed. If a roach ran the maze three times in succession without making an error, it was considered to have solved it. After each trial, the surface and the edges of the maze were painted with alcohol to remove any odor that might have been deposited by the roach.

For convenience, the errors made were grouped under two heads: those which resulted in the roach falling into the water and those made by the roach while remaining on the maze.

Under the first head there are three subdivisions: (1) rushes into the water without attempting to run the maze, (2) falls into the water after the roach had begun to run the maze, and (3) jumps into the water. Under the second head there are two subdivisions: (1) entering blind alleys, and (2) moving in the wrong

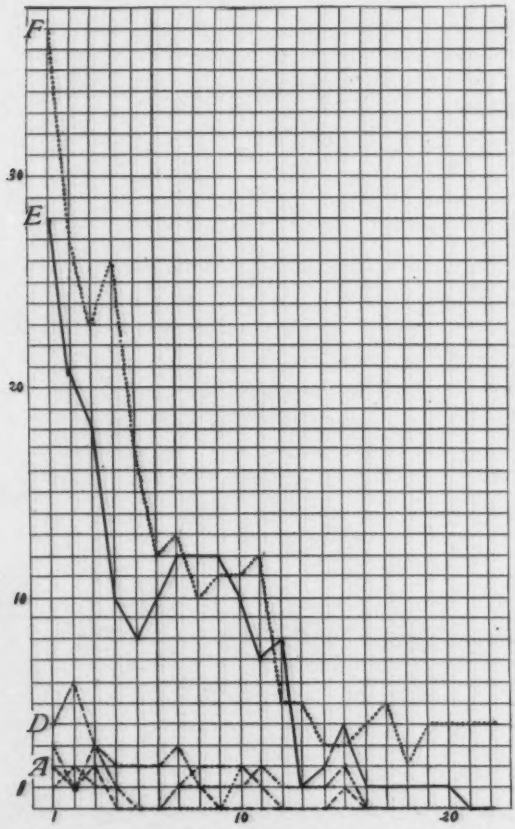

FIG. 3. Learning curves constructed from the average reactions of ten roaches. The spaces from right to left represent successive trials. *A*, the number of times the roach rushed into the water before beginning to run the maze. *B*, the number of times the roach fell into the water after beginning to run the maze. *C*, the number of times the roach jumped into the water. *D*, the total number of times the roach entered blind alleys. *E*, total number of errors made. *F*, total minutes required to run the maze.

direction along the right path. From the time the roach entered a blind alley until it returned to the right path was counted one error. If a roach which was moving in the wrong direction along the right path paused from time to time, each movement after a pause was counted an error. Movements, other than dashes into the water, which were made by a roach on *I* before it had entered the runway 1 were not counted; but once the roach had entered the runway 1, even though it returned to the starting platform *I*, all incorrect movements made by it were counted errors.

In my first experiments I arranged for the successive trials of each roach to come at intervals of several hours. This was done because I had an idea that experiments conducted at short intervals would produce fatigue effects which would vitiate the work. However, I soon found that the best results were obtained where the successive trials came at intervals of about half an hour and were continued throughout the working hours of a day. Towards the end of a long hot day such fatigue effects as a pronounced slowness of movement and the lapsing into errors that the roach had formed the habit of omitting would appear; but, on the whole, the repetition of trials at short intervals was much more satisfactory than the other method of experimenting.

Discussion of the Experiments.

Upon being placed on the maze for the first time, a roach almost invariably rushes off into the water. Upon being replaced on the maze, it usually repeats the performance; some, however, do not rush into the water a second time. Sooner or later it stops rushing into the water and begins to move around in search of some other means of escape. It moves to and fro along the runways, if paths with neither sides nor top may be called runways, enters blind alleys, occasionally falls into the water,[1] makes its toilet one or more times, perhaps engages in a few acrobatic stunts, and finally, by accident, discovers the incline and passes down it to the glass cell that is its home. The first time the roach is placed on the stage, this performance

[1] After it had fallen into the water, the roach was always replaced on the maze at the place from which it had its fall.

consumes from fifteen to sixty minutes. The next few trials the roach behaves in practically the same manner, but makes fewer and fewer mistakes. Finally, after a prolonged series of trials, in spite of frequent lapses, the mistakes are gradually eliminated and the roach runs the maze, without making any errors, in from one to four minutes. As the roach moves along, the antennæ are waving almost incessantly, as though seeking stimuli. The mistakes are eliminated so gradually that this may be considered a trial and error type of learning, if one may use that expression without predicating the absence of sensations and feelings. Such, in brief, is the behavior of the common roach on the maze; but one is impressed by the variations displayed.

These variations in behavior are of two types: differences due to age and modifications due to individuality. The older roaches usually move much more slowly and much more carefully than the younger ones. Roaches from ten to twelve millimeters long usually move so rapidly that they might well be called frisky. The slower gait of the older roaches is not due to feebleness, for they are fleet enough when placed on the floor of a room; but to what, in human beings, we call caution. As a result of this difference in speed, the younger roaches, on their initial trial, usually run the maze much more quickly than the adults; but, in doing so, make many more mistakes.

The variations due to individuality are the ones that are especially impressive. Some roaches, with humped backs, move sedately along in the middle of the runways, pausing at each corner to explore upward, outward and downward with their antennæ; others trot along in the middle of the runways, at first usually falling into the water at each angle, but later slowing up at the corners, exploring with their antennæ and moving onward. Some roaches, with their bodies extended until they are practically flat, drag themselves along so slowly that it taxes the patience of anyone who happens to be watching them; others, moving sometimes slowly and sometimes rapidly, always keep the claws of the legs of one side of the body in contact with the edge of the runway. When such a roach turns a corner it usually, although not invariably, crosses to the opposite side of the runway and clings to the edge with the legs of the corre-

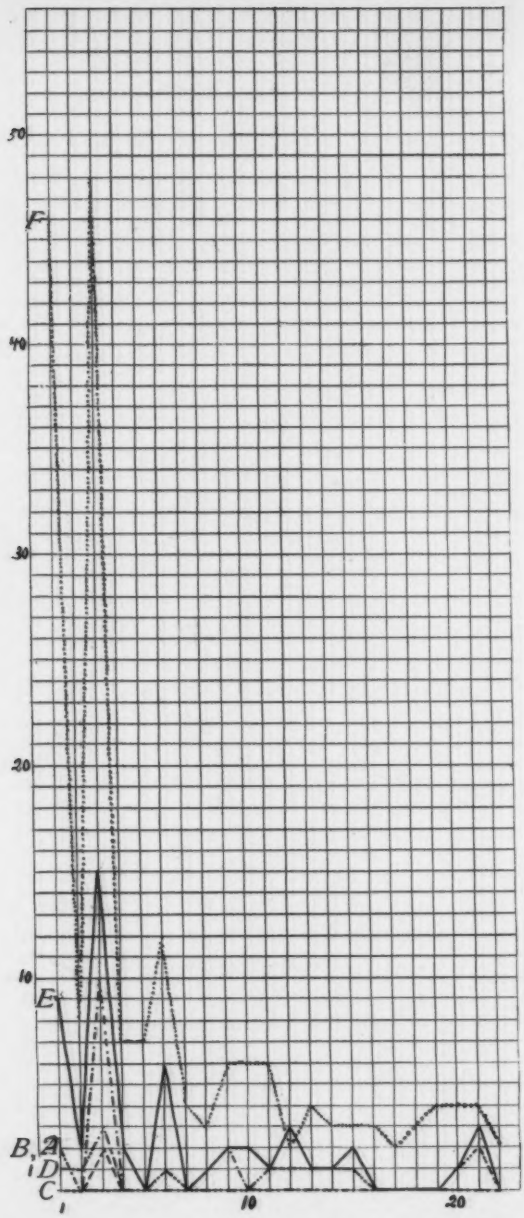

FIG. 4. Learning curves of a female roach 17 mm. long. The spaces from right to left represent successive trials. *A*, the number of times the roach rushed into the water before beginning to run the maze. *B*, the number of times the roach fell into the water after beginning to run the maze. *C*, the number of times the roach jumped into the water. *D*, the total number of times the roach entered blind alleys. *E*, total number of errors made. *F*, total minutes required to run the maze.

sponding side of its body. Some roaches pause at practically every point on the side of the runways and explore upward, outward, and downward with their antennæ, and then, retracing their steps, explore the same territory over and over again; yet other roaches pause only here and there to make explorations. Some roaches, and this is especially true of roaches from ten to fifteen millimeters in length, move along part of the time on top of the maze and part of the time suspended from its edge. Had the maze been constructed of cardboard these same roaches would have made part of their journey suspended from the bottom of the maze. Some roaches pause from time to time to make their toilet; others never once pause for such purposes. Some few roaches, after making several attempts to find an exit from the maze, stop trying and act as though they have given up all hope of succeeding; others, after failing to find a means of escape, attempt to jump to freedom. These jumping roaches were always returned to the maze at the point from which they jumped. After one to many jumps had proved failures, these roaches usually stopped jumping and proceeded to solve the maze in the right way. These variations were not inflexible instinctive responses, for the same roach did not always behave the same way at all trials.

Jumping Activities and Will.

Although this jumping activity results in a plunge into the water, it resembles neither the dashes into the water made by a roach on being placed on the maze for the first time nor the falls into the water by roaches that are trying to run the maze. The roach pauses at the edge of the maze and explores outward and downward with its antennæ. It acts as though it were trying to see something at a distance and then, after a pause, makes what an athlete would call a broad jump. Many roaches displayed this jumping behavior, but some were more prone to jump than others. I experimented with one roach which, on its initial trial, made ten jumps from the maze; usually from a different point each time. This jumping attitude is so characteristic that one can always predict when a roach is likely to jump. I say likely to jump instead of going to jump; because, after a roach has once

jumped into the water, the jumping attitude does not always result in a spring. To see a roach, which has learned to avoid rushing off of the maze into the water and which will struggle hard to avoid slipping from the edge of a runway into the water, halt, reach outward and upward with its antennæ, act as though it were trying to see what is beyond, pause and then jump is food for much thought. Have we not here a conflict of impulses and is not the jumping or the refusing to jump the resultant of this conflict? Is not such a resultant what the human psychologists call an act of will? Whenever I behold the jumping behavior, I am impressed with a feeling that the roach is experiencing a conflict of impulses and hence is displaying a will.

In most cases the jumps were made from some one of the outer edges of the maze; but, in a few cases, the jump seemed to be aimed at a definite point. On two occasions a roach jumped and landed on the cork of one of the bottles that supported the maze. At another time, a roach jumped from the runway 2 to blind alley *G* and traveled along that, over zigzaging pathways, to the main trail at *C* and thence to the incline and down it to its cell. On its next trial, the roach attempted to make this same leap; but only its forefeet touched *G* and it fell into the water. On two other occasions I noticed roaches attempt to jump from one runway to another; but they always failed to secure a foothold.

Acrobatic Feats.

The broad jumps described above are not the only acrobatic activities of the roaches that ran the maze. As mentioned above, the roaches frequently moved along suspended from the edge of a runway. With the three feet of one side clinging to the edge of the maze and with the three feet of the other side braced against the under side of the runway, any of the roaches could progress for a short distance, and the young roaches, those from ten to twelve millimeters in length, would run along in this position and return to the upper side at pleasure. In this inverted position, the young roaches could even turn around without returning to the upper side of the runway. Letting go of the edge of the maze with the first and second feet of the off side and catching hold of the edge with the third foot of the

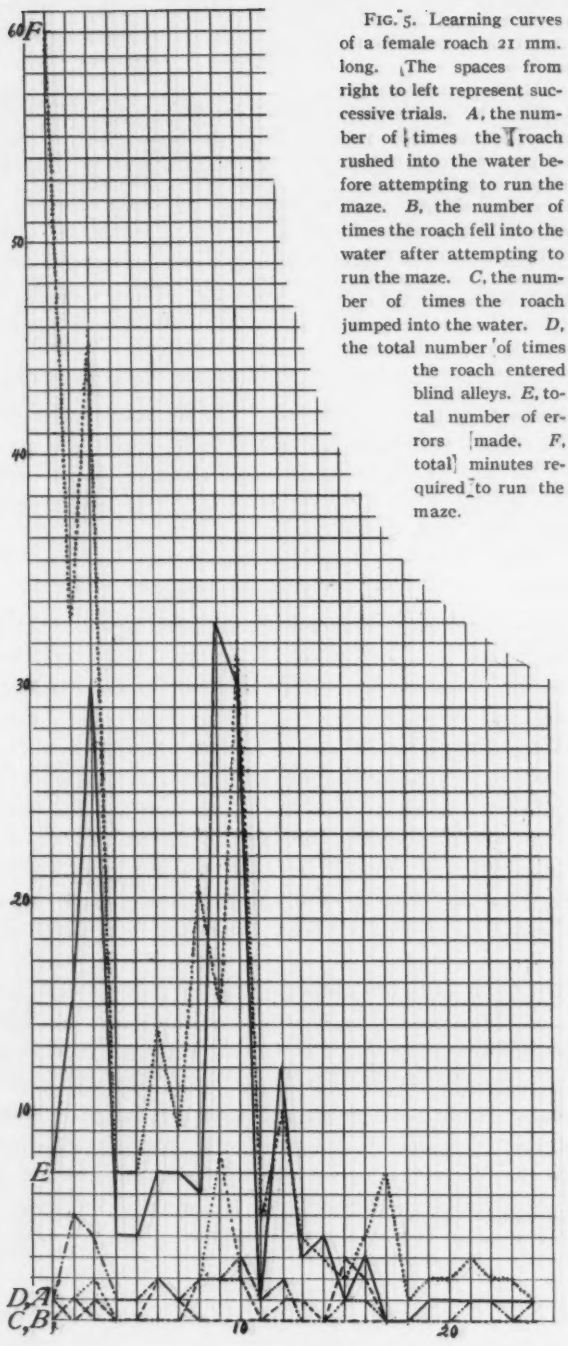

FIG. 5. Learning curves of a female roach 21 mm. long. The spaces from right to left represent successive trials. *A*, the number of times the roach rushed into the water before attempting to run the maze. *B*, the number of times the roach fell into the water after attempting to run the maze. *C*, the number of times the roach jumped into the water. *D*, the total number of times the roach entered blind alleys. *E*, total number of errors made. *F*, total minutes required to run the maze.

inner side, the roach would swing around on the underside of the maze until it could catch hold of the edge with the first and second feet of what had been the inner side. It then would remove the third foot of what had been the outer side and move along in the opposite direction. It was a common thing for roaches ten to twelve millimeters long to rest suspended beneath the maze with the claws of the third pair of legs clinging to the edge of a runway and with the other feet braced against its undersurface.

Frequently a roach was noticed making its toilet while suspended from the maze by one foot. On one occasion I observed a roach, about seventeen millimeters long, which was hanging suspended from the maze by its right third leg, brace itself by bringing the left third leg in front of the other and clinging to the edge of the maze with both feet.

Toilet-Making Habits.

I stated above that frequently movements to solve the maze are interrupted by toilet-making activities. Since most people look upon roaches as nasty things, this toilet-making behavior is a surprisingly interesting instinct. The mouth-parts, the first pair of legs and the third pair of legs are the instruments used by the roach in making its toilet and each has its special work. In cleaning the head and the base of the antennæ the first pair of legs are used in much the same way that a cat uses her forelegs in washing her face. One of the flexed legs is rubbed downward over the head and the base of the antennæ one or more times and then cleaned by the mouth-parts. This may be repeated several times.

As would be naturally expected, the antennæ, which seem to be the most important sense organs of the roach, are cleaned oftener than any other part. If you are standing a short distance from a roach that is resting on the maze, you will notice an antenna suddenly bend downward into the mouth. Slowly it straightens itself while the constantly moving mouth-parts remove the dirt. The next moment the antenna of the other side suddenly bends downward and is treated in the same way. One day a rather keen observer, who was visiting my insectary,

was sitting about a yard from a roach that was making her toilet. Suddenly he exclaimed: "What powerful muscles those slender antennæ must contain." Those antennæ do contain muscles which are used in waving them in search of stimuli; but those muscles are far too weak to bend the antennæ into the mouth of the roach. Had that visitor looked a little more keenly he would have seen the roach bow its head, dart one of its forelegs forward, catch in its bend the antenna of the other side and bend it downward to the mouth.

Sometimes, after a plunge into water, the antennæ become so wet that they are held together by capillary attraction and extend forward and upward like the horn of a unicorn. In that position they are out of the range of both of the forelegs. It is interesting to watch the energetic and unavailing efforts of such a roach to clean its antennæ. Standing on its second and third legs with the front part of the body elevated, it moves first one foreleg and then the other after the antennæ in such rapid succession that it resembles a gymnast taking arm exercises.

The palps of the maxillæ and of the labium are cleaned by the mouth-parts; but each palp is flexed into the mouth by its own muscles.

The body assumes a characteristic attitude while the legs and the ventral side of the body are being cleaned by the mouth-parts. Supported by the three legs of one side and by the hind leg of the other, the roach, with the side supported by one leg elevated at the expense of the other, reaches underneath her body and gives her legs and it a good cleaning with her mouth-parts. Again one is reminded of the behavior of a cat making her toilet.

To clean the dorsal surface of the abdomen, the roach uses first one hind leg and then the other as a scraper or brush. With these same legs the cercopods are thoroughly cleaned. In this cleaning process the spines on the legs are quite serviceable.

Sensations.

Plans have been formed to test rather thoroughly the senses of the roach; but, since it will be a long time before the tests can be completed, it is thought best to publish the following preliminary account.

Tactile.—The tactile sense of the roach is remarkably keen. Even a slight jar to one portion of the maze is responded to by a sudden more or less prolonged halt on the part of the roach on a distant point on the maze; and this is true when neither antennæ nor palpi are touching the maze and even when the antennæ have been amputated.

Olfactory.—On the maze itself no conclusive evidence was obtained of the use of this sense. True the antennæ were almost continually waving in space, but it was impossible to determine whether they were seeking olfactory or tactile stimuli. The trap used in capturing the roaches for these experiments was similar to the Graham roach trap described by F. L. Washburn in the *Journal of Economic Entomology* for June, 1913; but I used an eight-ounce bottle instead of an Erlenmeyer flask and no hairs were placed around the apex of the smaller cone. A trap baited with dry oatmeal flakes would capture practically no roaches; but one baited with oatmeal steeped in stale beer invariably captured large numbers. It seems reasonable to assume that it was the sense of smell that enticed the roaches into the trap.

Auditory.—Up to now my notes on the auditory sense are exceptionally non-committal. On the maze roaches seem to pay no attention to sounds produced continuously. For example, a loudly ticking clock was placed two feet from the maze; but to its sounds the roaches made no responses whatever. To certain suddenly produced sounds they responded by halting suddenly, to others they made no response. For example: one day while some tinners were fixing the guttering of a nearby house, to certain noises made by the tin the roaches were quite responsive; but, when, by means of a small bell, I attempted to demonstrate that they respond to suddenly produced sounds, the roaches made absolutely no external responses. By means of a Galton whistle and other methods an attempt is being made to solve the problem; but, up to now, no satisfactory solution has been reached.

Vision.—That the roach possesses vision of some kind is certain, and at times a roach would act as though it were able to distinguish objects at a distance. Recall roaches jumping from one runway to another—a distance of an inch and a half—

and roaches jumping from the maze to the top of a nearby bottle. Yet I could bring a pencil to within a centimeter of the head of a roach without causing a response unless I touched one of the antennæ.

Conclusions.

1. By arranging the trials at intervals of half an hour, a roach may be taught, within a day, to run the maze.

2. The gradual manner in which it eliminates its errors would cause one to say the roach learns to run the maze by the trial and error method; yet, in so doing, it utilizes sense stimuli. This is evidenced by the careful manner in which it examines (often over and over again) the corners and edges of the maze and the space adjacent thereto.

3. At times the roach acts as though experiencing the emotion the psychologists call will.

4. Although the effects of training persist for a long time, yet the memory of the roach is poor; for after an interval of twelve hours marked lapses were noticed.

5. In its toilet-making activities the behavior of the roach resembles very much the toilet-making activities of the cat.

6. In their behavior on the maze roaches display marked individuality.

TABLE I.

Successive Trials.	Date.	Number of Hours that Have Elapsed Since the Beginning of the Last Trial.	Errors Due to Movements on the Maze.						Errors which Caused the Roach to Fall into the Water.				Number of Times it Stopped to Make its Toilet.	Total Minutes Required to Run the Maze.
			By Entering Blind Alleys.				Movements in the Right Path, but in the Wrong Direction.	Total.	The Number of Times it Rushed into the Water before Beginning to Run the Maze.	The Number of Times it Fell into the Water After Beginning to Run the Maze.	The Number of Times it Jumped into the Water.	Total.		
			I. (Fig. 1, *A*.)	II. (Fig. 1, *B*.)	III. (Fig. 1; 8, *D*, *E*.)	IV. (Fig. 1; 9, 10, 11, *F*, *G*.)								
1	Aug. 7, 3:55 P.M.	0	0	0	1	0	5	6	1	0	0	1	19	60
2	Aug. 8, 8:02 A.M.	16¼	3	0	1	1	13	18	0	1	1	2	24	33
3	Aug. 9, 6:54 A.M.	23	3	0	0	0	24	27	1	0	2	3	24	46
4	Aug. 10, 8:08 A.M.	24¼	0	0	1	0	3	4	0	0	0	0	0	7
5	Aug. 10, 6:53 P.M.	10¾	1	0	0	0	3	4	0	0	0	0	1	7
6	Aug. 11, 7:52 A.M.	13	1	0	1	0	3	5	2	0	0	2	8	14
7	Aug. 11, 2:05 P.M.	6¼	0	0	1	0	5	6	1	0	0	1	4	9
8	Aug. 11, 3:22 P.M.	1¼	0	0	1	1	0	2	0	2	2	4	10	21
9	Aug. 12, 7:23 A.M.	16	1	1	0	0	15	17	0	8	8	16	4	15
10	Aug. 12, 8:06 A.M.	0¾	2	0	1	0	23	26	0	2	2	4	9	32
11	Aug. 12, 9:16 A.M.	1¼	0	0	1	0	0	1	0	0	0	0	0	5
12	Aug. 12, 10:18 A.M.	1	1	1	0	0	7	9	1	0	1	2	3	10
13	Aug. 12, 12:46 P.M.	2¾	0	0	0	0	1	1	1	0	1	2	4	4
14	Aug. 12, 12:54 P.M.	0¼	0	0	0	0	4	4	0	0	0	0	2	3
15	Aug. 12, 1:20 P.M.	0½	0	0	1	0	0	1	3	0	0	3	4	2
16	Aug. 12, 1:33 P.M.	0¼	0	0	1	0	0	1	2	0	0	2	2	4
17	Aug. 12, 2:29 P.M.	1	0	0	0	0	0	0	0	0	0	0	2	7
18	Aug. 12, 2:58 P.M.	0¼	0	0	0	0	0	0	0	0	0	0	4	1
19	Aug. 12, 3:34 P.M.	0¼	0	0	0	0	1	1	0	0	0	0	1	2
20	Aug. 12, 4:01 P.M.	0¼	0	0	0	0	1	1	0	0	0	0	1	2
21	Aug. 13, 6:04 A.M.	14	0	0	1	0	0	1	0	0	0	0	2	3
22	Aug. 13, 6:45 A.M.	0¾	1	0	0	0	0	1	0	0	0	0	1	2
23	Aug. 13, 7:08 A.M.	0¼	0	0	0	0	1	1	0	0	0	0	0	2
24	Aug. 13, 8:03 A.M.	1	1	0	0	0	0	1	0	0	0	0	0	1

This is a compilation of the reactions of the first ten roaches examined. Throughout the first part of this series of experiments a long rest was given after each trial.

TABLE II.

Successive Trials.	Date.	Number of Hours that Have Elapsed Since the Beginning of the Last Trial.	Errors Due to Movements on the Maze.						Errors which Caused the Roach to Fall into the Water.				Number of Times it Stopped to Make its Toilet.	Total Minutes Required to Run the Maze.
			By Entering Blind Alleys.				Movements in the Right Path, but in the Wrong Direction.	Total.	Number of Times it Rushed into the Water Before Attempting to Run the Maze.	Number of Falls into the Water After Beginning to Run the Maze.	Number of Jumps into the Water.	Total.		
			I. (Fig. 1, *A*.)	II. (Fig. 1, *B*.)	III. (Fig. 1: 8, *D*, *E*.)	IV. (Fig. 1: 9, 10, 11, *F*, *G*.)								
1	Aug. 8, 9:30 A.M.	0	1	0	1	1	0	3	2	10	0	12	13	45
2	Aug. 14, 5:46 A.M.	130½	1	0	0	0	4	5	2	2	0	4	9	48
3	Aug. 14, 7:04 A.M.	1½	0	0	1	0	1	2	0	0	0	0	0	8
4	Aug. 14, 7:31 A.M.		0	0	0	0	2	2	0	0	0	0	0	7
5	Aug. 14, 8:03 A.M.		0	0	0	0	0	0	0	0	0	0	0	7
6	Aug. 14, 8:40 A.M.		0	0	1	0	0	1	0	5	0	5	4	12
7	Aug. 14, 9:02 A.M.		0	0	0	0	0	0	0	0	0	0	1	4
8	Aug. 14, 9:37 A.M.		0	0	0	0	0	0	0	1	0	1	0	3
9	Aug. 14, 10:14 A.M.		0	0	0	0	0	0	0	2	0	2	0	6
10	Aug. 14, 10:42 A.M.		0	0	0	0	2	2	0	0	0	0	3	6
11	Aug. 14, 11:18 A.M.		1	0	0	0	0	1	0	0	0	0	0	6
12	Aug. 14, 11:45 A.M.		1	0	0	0	2	3	0	0	0	0	0	2
13	Aug. 14, 12:16 P.M.		0	0	1	0	0	1	0	0	0	0	2	4
14	Aug. 14, 12:46 P.M.		0	0	1	0	0	1	0	0	0	0	2	3
15	Aug. 14, 1:08 P.M.		1	0	1	0	0	2	0	0	0	0	2	3
16	Aug. 14, 1:58 P.M.	1	0	0	0	0	0	0	0	0	0	0	1	3
17	Aug. 14, 2:28 P.M.		0	0	0	0	0	0	0	0	0	0	0	2
18	Aug. 14, 3:07 P.M.		0	0	0	0	0	0	0	0	0	0	6	3
19	Aug. 14, 3:50 P.M.		0	0	0	0	0	0	0	0	0	0	1	4
20	Aug. 14, 4:24 P.M.		1	0	0	0	0	1	0	0	0	0	1	4
21	Aug. 15, 5:30 A.M.	13	1	0	0	1	0	2	1	0	0	1	2	4
22	Aug. 15, 5:46 A.M.	½	0	0	0	0	0	0	0	0	0	0	0	2
23	Aug. 16, 6:35 A.M.	24½	0	1	0	0	0	1	6	0	0	6	2	12

This table records the reactions of a female roach 21 mm. long. Throughout this series of experiments the rest period between the experiments was short.

TABLE III.

Successive Trials.	Number of Hours that Have Elapsed Since the Beginning of the Last Trial.	Errors Due to Movements on the Maze.						Errors which Caused the Roach to Fall into the Water.				The Number of Times it Stopped to Make its Toilet.	Total Minutes Required to Run the Maze.
		Due to Entering Blind Alleys.				Movements in the Right Path but in the Wrong Direction.	Total.	The Number of Times it Rushed into the Water Before Beginning to Run the Maze.	The Number of Times it Fell into the Water After Beginning to Run the Maze.	The Number of Times it Jumped into the Water.	Total.		
		I. (Fig. 1, *A*.)	II. (Fig. 1, *B*.)	III. (Fig. 1; 8, *D*, *E*.)	IV. (Fig. 1; 9, 10, 11, *F*, *G*.)								
1	0	2	0	2	0	18	22	2	3	1	6	13	37
2	18½	2	0	3	1	9	15	1	1	2	4	6	27
3	16	2	0	1	0	10	13	2	2	1	5	7	23
4	16½	1	0	1	0	6	8	0	1	1	2	7	26
5	11½	0	0	1	1	6	8	0	0	0	0	4	17
6	5	1	0	1	0	7	9	0	1	0	1	3	12
7	4½	1	0	2	0	7	10	1	1	0	2	9	13
8	1½	0	0	1	0	2	3	1	2	0	3	5	10
9	9½	1	0	0	0	9	10	0	2	0	2	2	11
10	3½	1	0	0	0	6	7	0	2	2	4	7	11
11	1	1	0	0	1	2	4	0	1	1	2	4	12
12	1	1	0	0	0	6	7	0	0	0	0	2	5
13	1½	0	0	1	0	0	1	0	0	0	0	2	5
14	1	0	0	1	0	1	2	0	0	0	0	2	3
15	1	1	0	1	0	1	3	1	0	0	1	3	3
16		0	0	0	0	1	1	0	0	0	0	1	4
17		0	0	0	0	1	1	0	0	0	0	1	5
18		0	0	0	0	1	1	0	0	0	0	5	2
19		0	0	0	0	1	1	0	0	0	0	1	4
20		0	0	0	0	1	1	0	0	0	0	2	4
21		0	0	0	0	0	0	0	0	0	0	2	5

This table records the reactions of a young female roach 17 mm. long. Throughout the first part of the series the rest period between two trials was long.

TABLE IV.

Successive Trials.	Date.	Number of Hours that Have Elapsed Since the Beginning of the Last Trial.	Errors Due to Movements on the Maze.						Errors which Caused the Roach to Fall into the Water.				Total Minutes Required to Run the Maze.	The Number of Times it Stopped to Make its Toilet.
			Due to Entering Blind Alleys.				Movements in the Right Path, but in the Wrong Direction.	The Number of Times it Rushed into the Water Before Beginning to Run the Maze.	The Number of Times it Fell into the Water After Beginning to Run the Maze.	The Number of Times it Jumped into the Water.	Total.	The Number of Times it Stopped to Make its Toilet.		
			I. (Fig. 1, *A*.)	II. (Fig. 1, *B*.)	III. (Fig. 1; 8, *D*, *E*.)	IV. (Fig. 1; 9, 10, 11, *F*, *G*.)								
1	Aug. 8, 9:13 A.M.	0	0	0	1	0	13	14	1	2	2	5	9	14
2	Aug. 9, 8:19 A.M.	23	1	0	1	1	5	8	1	2	1	4	6	26
3	Aug. 9, 1:43 P.M.	5½	0	0	0	0	0	0	1	0	0	1	2	3
4	Aug. 10, 6:57 A.M.	17¾	1	0	1	0	9	11	0	3	3	6	18	57
5	Aug. 10, 11:18 A.M.	4¼	0	0	1	0	5	6	0	0	0	0	2	21
6	Aug. 10, 2:52 P.M.	3½	1	0	0	0	8	9	0	1	0	1	1	11
7	Aug. 10, 4:26 P.M.	1½	2	0	3	0	17	22	1	0	0	1	23	22
8	Aug. 10, 6:30 P.M.	2	1	0	1	0	6	8	0	0	0	0	3	6
9	Aug. 11, 5:40 A.M.	11¼	1	0	1	0	13	15	0	0	0	0	3	18
10	Aug. 11, 7:00 A.M.	1¾	1	0	1	0	7	9	0	1	1	2	5	12
11	Aug. 11, 8:23 A.M.	1½	3	0	1	1	13	18	2	0	2	4	10	23
12	Aug. 11, 10:54 A.M.	2½	2	0	1	0	5	8	0	0	0	0	5	7
13	Aug. 11, 1:23 P.M.	2½	0	0	1	1	1	3	0	0	0	0	0	7
14	Aug. 11, 2:00 P.M.		1	0	1	0	1	3	0	0	0	0	2	2
15	Aug. 11, 2:29 P.M.		0	1	1	0	5	7	0	0	0	0	3	5
16	Aug. 11, 3:12 P.M.		1	0	1	0	8	10	0	0	0	0	1	7
17	Aug. 11, 3:46 P.M.		0	0	0	0	8	8	0	0	0	0	1	9
18	Aug. 11, 4:37 P.M.		1	0	1	0	5	7	0	0	0	0	2	2
19	Aug. 12, 6:02 A.M.	13½	1	0	1	0	7	9	0	0	0	0	6	22
20	Aug. 12, 6:30 A.M.		0	0	0	0	3	3	0	4	0	4	3	12
21	Aug. 12, 6:56 A.M.		1	0	1	0	2	4	0	4	0	4	6	13

This table records the reactions of a female roach 10 mm. long which after 21 trials had displayed no ability to learn the maze. It learned to avoid falling into the water; but displayed no ability to avoid making errors on the runways. It finally gave up attempting to learn the maze and tried to jump to freedom. The roach was accidentally killed at the close of the 21st experiment. Its reactions are recorded because it was the most unapt roach that I had.

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